THE ZOOLOGIST

No. 878.—August 15th, 1914.

GENERAL REMARKS ON SOME POINTS IN THE LIFE-HISTORY OF THE SALMON, AND A CONTRAST OF ITS OVIPOSITION WITH THAT OF A FEW OTHER TYPES OF TELEOSTEANS.

By Prof. McIntosh, M.D., LL.D., F.R.SS. L. & E., Gatty Marine Laboratory, University St. Andrews.

Few fishes, either now or formerly, have attracted more attention than the Salmon, for it is conspicuous alike by the beauty and symmetry of its form and the celerity of its movements, which are seen to advantage in the clear currents of the rivers which it periodically haunts. But both the naturalist and the anatomist might have celebrated its physical perfection in vain if there had not been other qualities which enhanced it in the estimation of man, such as the rich nature of its muscle as food, its high price, and the zest with which it is followed for sport—all which have brought it continually under the eyes of experienced observers, and thus information concerning it has been extended in a remarkable degree.

The Salmon is essentially a fish of the present waters, for it goes no further back than the Pleistocene times, and, as a bony fish, it is characterised by the occurrence of fins with soft rays and of one (the adipose or "fatty" fin) without any, its simple large air-bladder has an open pneumatic duct, and its scales are cycloid, like those of the Eel, Herring, and Pilchard. Its bones, as becomes a fish which partly frequents fresh water, are lighter or less ossified than such as the Cod or the Plaice; and its skull has much cartilage in its composition. Its lateral

muscles are of great power, a provision which enables it to overcome the cataracts and cascades of rivers, for, curving itself, it suddenly contracts the muscles of the convex side and throws its weighty body out of the water to a considerable height. When fancy held its sway in natural history, the older authors suggested that it rested its body on a rock, or in other cases put its tail in its mouth so as to get full benefit of the sudden muscular contraction in its leaps. This muscle has a characteristic tint from the oil, and the same hue is present in the globules which occur below the blastoderm in the developing egg. As in other fishes these great muscles long retain their irritability, so that by making slits and immersing the fish in cold water a stale fish is rendered firm.

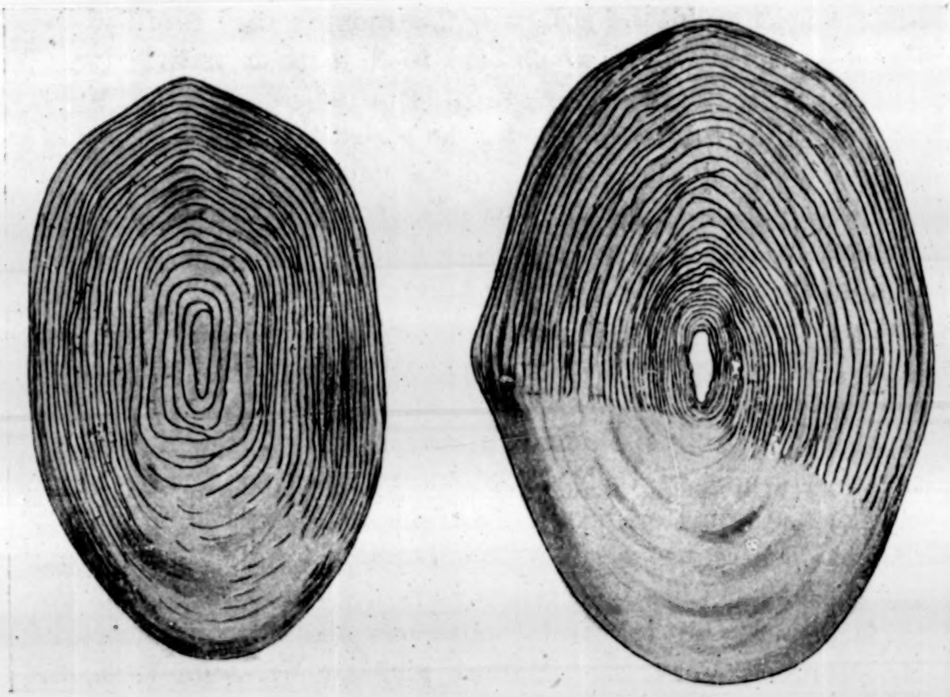
Like most fishes the Salmon is a predatory form, yet little or no food has been found in its stomach in fresh water, a fact which has led to various explanations by the public and by scientific men. Thus Prof. Owen at one time thought that, in common with many other fishes when hooked or netted, it emptied its stomach by an instinctive act of fear or to facilitate escape by lightening its load, leaving only minute animalcules in the gastric mucus. But, as pointed out long ago, if this were the rule, the intestine would be well filled, since the Salmon cannot eject its food after it passes the pylorus; moreover, the very terror which impels the action in one fish may paralyze the efforts in another. Investigations in the Tay below Perth from the Tents Moor upward show that many Sand-Eels, Sprats, Herrings, crustaceans, disintegrating muscular tissue, lime-crystals, and the ordinary chymous mass occur in the stomach of certain Salmon which probably fed in the sea or in the estuary. Sand-Eels, indeed, form a favourite bait in the sea for Salmon, and it is stated that in Sutherland hooks baited with this fish are attached to a bladder which is allowed to float up a narrow firth for its capture. The contrast with such as the Sparling and the Salmon-Trout, which are both caught by nets, is marked, for their stomachs are generally well filled. The Salmon, indeed, does not feed in fresh water, the fat and other materials stored in its muscles and viscera sufficing for the full development of its reproductive organs in the rivers in which it spawns.

It is noteworthy that within the last thirty years, probably less, our notions of the life-history of this fish have been greatly modified, especially as to its sojourn in the sea. Thus during the twenty-three years—from 1860 to 1882—the prevailing opinion was that some of the young (called Parr) became silvery fishes (Smolts) at the end of the first year, which Dahl still holds is the rule for Norway, and that all became so at the end of the second year, and migrated to the sea. Further, that after a sojourn in the sea of a few months they returned as Grilse of some pounds weight ($1\frac{1}{2}$ to 5) to their native rivers. This view (as to the speedy return from the sea) was held to be proved by the capture of those from which the "fatty" fin had been removed on their issue from Stormontfield ponds. There can be no doubt that my old friends, Mr. Robert Buist and Mr. William Brown, were quite right in holding that the "fatty" fin is not reproduced; but, on the other hand, it may be asserted that other agencies than scissors might have bereft a few of this organ. The modern method of placing a loop of silver wire in the dorsal fin admits of no doubt, and it has now been shown that the young Smolts remain a year or more (three) in the sea before returning to their early haunts to spawn. It is held, indeed, that some are fishes of considerable size before leaving the sea—where, of course, it is impossible for them to spawn, and these constitute the various runs of Salmon so well-known to tacksmen and to careful observers like Mr. Calderwood, Mr. Moreton Frewer, Mr. Malloch, the late Mr. John Dickson, of Perth, and others.

Quite recently, also, the intimate structure of the scales of the Salmon at various ages has facilitated more accurate knowledge of its age and habits. When dealing more than fifty years ago with the Salmon of the Tay and figuring the scales of Salmon and of Smolt, it was pointed out and figured that the concentric rings in the latter were few, and that there was scarcely a blank at the free end; whereas in the former the rings greatly increased in number, and the smooth portion at the free edge was of considerable size. The question of grouping the rings into annual series had not then been inquired into, and the spawning mark was unknown. (Figs. 1 and 2.)

Recently many writers have devoted special attention to

these scales as an index to the age and spawning periods of the fishes, such as W. Calderwood, A. T. Masterman, H. W. Johnston, Eisdale, Dahl, Malloch, and others. No communication, however, deals with the subject in a more thorough manner than that of Dr. A. T. Masterman, Superintending Inspector for Fishery Investigations.* His observations are illustrated by excellent figures. He concludes that the scales are retained



FIGS. 1 and 2.—Scales of Smolt and Salmon from the Tay, reduced from two lecture-drawings made in 1862 from life. I am indebted to the Carnegie Trust for the reduction of these figures.

throughout life and grow in a differential manner correlative with the seasons; the small number of the ridges in the Smolt-scale remain unaltered in the centre of the adult scale; cessation of growth takes place on return to the river, and on the attainment and the duration of a condition of physiological repletion, usually at the commencement of the second, third, or subsequent winter in the sea. He holds that the scale is not available for estimation of the period of time spent in the river after the

* 'Board of Agriculture and Fisheries Investigations,' series i. vol. i., "Salmon and Freshwater Fisheries," 1913.

return. During development of the reproductive organs the scales suffer deterioration—producing the "spawning mark."

Though the Salmon is chiefly known as a freshwater fish, yet it is as much, if not more, an inhabitant of the sea, and to this habit there can be little doubt its safety is mainly due. It seeks the fresh waters for the most part to reproduce its species, for it does not enter them to feed. In the stomach of those caught off Tentsmuir and at the entrance to the Tay, as already stated, Sprats, Herrings and Sand-Eels occur, but after they have fairly entered fresh water no food of note is taken.

Whilst the Salmon feeds freely in the sea it also becomes a prey to larger forms, such as Seals, toothed Whales of various kinds, even a Cachalot occasionally taking one. Groups of Seals at the estuaries of Salmon-rivers, such as the Tay, cause considerable loss to the tacksmen, who wage war againt them. Ca'ing Whales (*Globiocephalus melas*) appear to search for Salmon in their course round the various stake-nets in a bay, and the fishermen think the Porbeagle Sharks and Porpoises captured in these nets likewise seek the Salmon, but no fragments of Salmon have ever occurred in either at St. Andrews.

As a rule Salmon are captured in the sea by stake-nets (or fly-nets) on sandy beaches, and by bag-nets off rocky shores. The principle in both is similar. At St. Andrews the stake-net, in use for generations on the west sands,* consists of a vertical leader (a single stretch of net) run out from the shore, supported on stakes or poles, and terminating seawards in two chambers; the first opening freely on each side of the leader, but otherwise closed, so that a fish passing in either direction parallel with the shore is guided into it, then into the second chamber by a narrow defile, and lastly into the "trap" by a similar defile. Entrance is easy, but the acuteness of the fish is seldom sufficient for escape. The retiring tide carries many other fishes into the netted chambers, such as Flounders (*P. flesus*), young Turbot, Brill, Plaice, Sturgeon, Dog-Fishes, Frog-Fishes, young Sharks and Skate; whilst Porpoises, young Ca'ing Whales, or even a *Regalecus* and a Great Northern Diver are some-

* A water-colour drawing of which (by R. M.) is in the Gatty Marine Laboratory. The net is usually erected in May after the heavy surf of early spring disappears.

times procured. The small size of the valuable young Turbot so often captured has frequently been noticed, especially as they are only utilised as bait for Crabs. Such ought to be liberated as soon as the "trap" is exposed at low water. To save trouble, the stakes to which the poles of the leader are fixed are left permanently in the sand, and are usually favourite sites for the borings of *Limnoria*.

The bag-nets are similar in structure, only they are anchored off the rocky shores all round Great Britain and Ireland, and also have an inner and an outer chamber distended by poles, and a trap to which the leader guides the Salmon. These nets appear to be most successful in August, and, in addition to capturing Salmon, their ropes and floats afford a favourite site for the fixation of the planulæ of *Obelia*, the larvæ of *Balani*, and myriads of the young of the Mussel after their pelagic stage. The fishermen row from the shore at intervals, release the outermost stake, and then hauling the net (trap) up to the side of the cable "a lacing at the side of the inner court is opened, and the fish allowed to slide into the boat."* It is said that few other fishes than Salmon are captured in these nets, but this needs qualification, for from early times the fishermen on the north-eastern coasts of Scotland fed their Pigs on the swarms of Lump-Suckers thus secured, and the same is found at St. Andrews, where many an interesting fish such as Mackerel, Rock-Herring, Horse-Mackerel, Conger, Sea-Perch, Frog-Fishes, Skate, Piked Dog-Fishes, Sharks, Mullet, besides Guillemots, young and old Porpoises, and even the long bands of tough mucus holding the eggs of the Frog-Fish have been procured from these nets.

The life of the Salmon in the sea is still more or less shrouded in mystery, for it is rarely captured in the off-shore waters. Yet trawlers occasionally secure fine examples in deep water in their nets, and so do the inshore fishermen with their trammel-nets. Reports as to the nature of the food found in these examples are still desiderata. During several months' observations off shore in 1884, only one fine Salmon was seen leaping above the surface many miles from land.

* *Vide* recent description by Mr. Calderwood, 'S. F. B. Report, Salmon Fisheries,' 1913, pp. 3–4.

Young Salmonoids, about a foot in length or somewhat less, the size of a Herring,* however, were caught in the Herring nets in August, and this fifty miles from shore. Such an occurrence affords little information, however, as to the numbers in an area, for only those of a suitable size are meshed; and in many cases the capture of the adults by liners and trawlers is not reported. Mr. Calderwood,† H.M. Inspector of Salmon Fisheries, alludes to several captures at sea by trawlers, and the experiments which are being carried out by him in marking Salmon obtained in bag-nets at sea will, it is hoped, considerably add to our knowledge in the near future. Salmonoids considerably larger than Smolts are occasionally captured in numbers in the estuary of the Tay, so that such forms must linger now and then inshore.

Whilst food is thus generally absent from the alimentary canal of the Salmon, parasites are plentiful. Numerous tapeworms occupy the pyloric cæca, and threadworms crawl forward into the stomach on the death of the host, or are coiled on the surface of the viscera and mesentery. Distomes press their soft bodies amongst the mucus, their pale fluid passing backward and forward, becomes stationary and again proceeds. *Echinorhynchi* are attached to the wall of the stomach by their proboscides. In the duodenum are many larval Distomes, which move actively in the mucus.

In connection with the circulation and respiration there is little differentiation from the ordinary Teleostean. It is worthy of note, however, that in the young fish the first vessels to leave the line of the body are those passing into the "fatty" fin; whilst in fresh water the gills have the parasite *Lernæopoda salmonea*, which is killed when it enters the sea, just as the external parasite *Lepeophtheirus salmonis* disappears in fresh water. No young fish is better adapted for experiments on the circulation than the Salmon, whether in connection with the effect of drugs and poisons, or the behaviour of the capillaries after operations. The presence of a dilatation on the caudal

* There may have been many larger and smaller accompanying the forms caught, the heads of the former being too large for entering the mesh, whilst the smaller heads might slip out.

† *Vide* 'S. F. B. Salmon Fisheries,' 1913, No. 1, pp. 4 *et seq*. (1914).

vein (so-called "heart") is another feature of interest, and the impulse of the heart causes a slight jerk in it on each contraction. In Shaw's figure in the Trans. Roy. Soc., Edinburgh, the vitelline vein runs behind instead of in front of the large oil-globules. The vessels of the yolk-sac do not branch very minutely, but enter the venous system by a current two or three discs broad.

Sooner or later, then, the Salmon leaves the sea and enters the mouths of certain rivers for the purpose of spawning, and so strong is the instinct which impells it, that, using the term Salmon in its widest sense, it sweeps through the whole length of the largest rivers, and, as is well known, reaches Bohemia by the Elbe, Switzerland by the Rhine, and the Cordilleras of America by the Amazon—the course of which is more than 2000 miles; and it has been stated that it reaches the sources of the river in about three months, but this appears to need verification, for Mr. Calderwood lately found that his marked fishes took ten days to cover sixty-eight miles, though of course it is unknown whether a straight course was followed. No country, however, shows on a more gigantic scale the impulse just mentioned than Canada, where the work of Dr. Edward E. Prince, the Dominion Commissioner of Fisheries, has lately thrown a flood of light both in regard to investigation and legislation.* The vast hordes of the various species of Salmon, for instance, which pour round Vancouver Island from the North Pacific to enter the clear, cold waters of the Fraser River, defies computation, and the phenomenon is still more remarkable when it is remembered that the majority in this instance perish after spawning. Even in our own waters the mortality after spawning is considerable.

In its course up a river to the pure rills and streamlets which form its source, the Salmon encounters many obstacles, such as precipitous falls, cascades and artificial obstructions, some of which can only be passed in high flood, whilst a few are impassable except by salmon-passes, early introduced by Mr. Smith of Deanston, and by Messrs. Ashworth in their Galway fishings. Moreover, it has to run the gauntlet of the endless

* The extent of these fisheries is well shown by a communication by Prof. Prince to the International Fisheries Congress at Rome in 1911.

series of legitimate trammel-nets and of poaching devices, especially at weirs; the attacks of Seals at the estuary and of Otters higher up, and the use of trained Dogs which endeavour to drive it into nets, and nothing terrifies a Salmon more than a Dog. Thus when the water was turned aside from a pass for examination on an Irish river, a Salmon of about 20 lb. floundered amongst the water in the shallows, and a terrier rushed at it, causing the fish in frantic terror to dash itself hither and thither until it gained a pool of some depth, where it lay alongside and parallel with the concrete wall in perfect quietude, permitting the point of a stick to rest on its back rather than move from its shelter and run the risk of meeting its enemy.

In former days before the syndicate took the fishings of the river Tay into their hands, one might well have doubts as to the safety of a sufficient number of fishes to stock the river. Thus, on looking down from Kinnoull Hill during the season, each bank of the river was dotted with the little huts for the fishermen, and the coble, as a black speck, pushed out everywhere into the stream—now from this bank and again from the other—the ripple of the boats' wake concealing the gradual falling of the net. The convexity of the boat's course, which was in the form of a loop, was directed downward (toward the mouth of the river) during ebb-tide, and the reverse during the flow of the tide. One end of the net was fastened to the boat, the other on shore to a stationary windlass, by which, at the end of the loop formed by the boat, the net was drawn to the bank, and the fishes removed from the bag or trap of the net and killed by blows from a stick. Now all this is changed, and the reduction of the number of the fishing stations has been found to be no disadvantage financially, though the lively and picturesque features of old can no more be seen. Yet, if the Salmon is persecuted by stake and bag-nets, by trawlers and by trammel-nets in the sea, it is pursued with tenfold avidity in fresh waters legitimately by nets of various kinds, sometimes with the aid of Dogs, by traps termed "cruives" in dam-dykes (now, it is to be hoped, almost in abeyance), by spears, and by anglers.

It was formerly held, and with good reason, that early or

late Salmon-rivers, as they were called, owed this feature to the temperature of their waters. Thus, in Britain, certain rivers arising from lochs are earlier than some which do not; Yarrell, for instance, quoting Sir William Jardine's case of the Oikel and the Shin in Sutherlandshire. The Oikel springs form a small alpine lake about half a mile in breadth, whereas the Shin, a tributary of the Oikel, takes its origin from Loch Shin, a large and deep loch connected to a chain of other deep lochs. Early in spring all Salmon entering the common estuary diverge up the Shin, and do not pass into the Oikel until later.

The eggs in the ovaries of the Salmon are developed so as to form a mass of several pounds, varying according to the size of the fish, on each side by the utilization of the nutriment stored up in the muscular and other tissues, as indeed had long been suspected, but more clearly demonstrated by Meischer Ruesch and Noel Paton.*

In the ovary, as in that of the Wolf-Fish (*Anarrhichas*), the eggs attain a comparatively large size, and, moreover, all reach maturity about the same time, so that they are shed within a limited period—a condition very different, for instance, from that in the Cod or Haddock. On entering a river some pass upward to the spawning-ground with considerable rapidity, whilst others, especially in the larger rivers, or in those with lakes, may remain many months before spawning, and their perseverance in overcoming natural obstacles in their ascent to suitable spawning-grounds is well known. Fishes are usually credited with small intelligence, but as a matter of fact their intelligence is keen. Both intelligence and instinct, and in some cases memory, come into play in the selection of a good spawning-bed of clean gravel—as at the Boat (now the Bridge) of Caputh. Few sights are more interesting to the naturalist than to watch the fishes swarming on such a spawning-bed in November. The quiet stretch of shallow water (for it is out of the main current) is alive with the dorsal fins of the males as

* It may be noted that before Dr. (now Professor) Noel Paton began his researches the late Mr. James Johnston, of Montrose, my colleague on the Fishery Board, agreed to present two Salmon per week for this purpose, and he loyally carried out his promise. Mr. Johnston deserves grateful remembrance for his generosity.

they rush after each other in their fight for the females, and here and there the surface is broken by the splash of a combat. The sight from the Bridge at Galway as the fishes pass up to their spawning-ground is also striking, but at a given moment they are far fewer than those collected on such a spawning-ground as that just mentioned. There the female stirs up the gravel with her tail, sheds the eggs in batches, probably during several days, and covers them over, the area being, as it were, sown with them, whilst the attendant male emits milt for fertilization. The newly extruded ova are covered with viscid mucus, which to some extent causes them to roll less readily on the stones, and prevents the current carrying them down-stream. Their specific gravity, moreover, is greater than that of the water, the reverse being the case in the pelagic eggs of the Cod and many others. Moreover, the eggs of the Salmon are shed into the cœlom, and thence out by the genital pore behind the vent, whereas the Cod has oviducts.

The developing egg remains in the gravel for 120 to 130 days or more, according to temperature, when the young fish is extruded. In a private apparatus in a bedroom (fig. 3) the young were hatched in sixty days.

The larval Salmon keeps to its gravelly bed for a month or six weeks, until its store of yolk is more or less exhausted; and then it swims freely as a little fish about an inch in length (called a Parr), though at first it keeps to hollows in the bed of the stream where the currents are less strong.

The destruction of ova in their natural spawning-beds is considerable by floods, Trout, Salmon-Trout, larvæ, beetles, birds, and other forms. Hence the basis on which hatcheries were advocated, and there is no doubt great benefit in many cases has resulted from the artificial rearing of Salmon to a certain stage. Yet if the adults are sufficiently protected on their spawning-beds (which unfortunately they are not in certain cases, *e.g.* Ireland), the need for hatcheries would be restricted. It is the serious obstruction by weirs or impassable falls and the too-severe netting, together with the interference with the fishes on their spawning-beds, which reduces the numbers in many fine rivers.

As the breeding-ponds at Stormontfield-on-the-Tay were

amongst the earliest and best known, it may not be out of place briefly to record the impression of a first inspection in May, 1861. They are situated on the ground of the Earl of Mansfield, and were constructed in 1854 by subsidies from the leading proprietors of the Salmon-fishings on the Tay, each paying in proportion to the extent of his fishings. They are economically constructed, the chief expense, indeed, being the

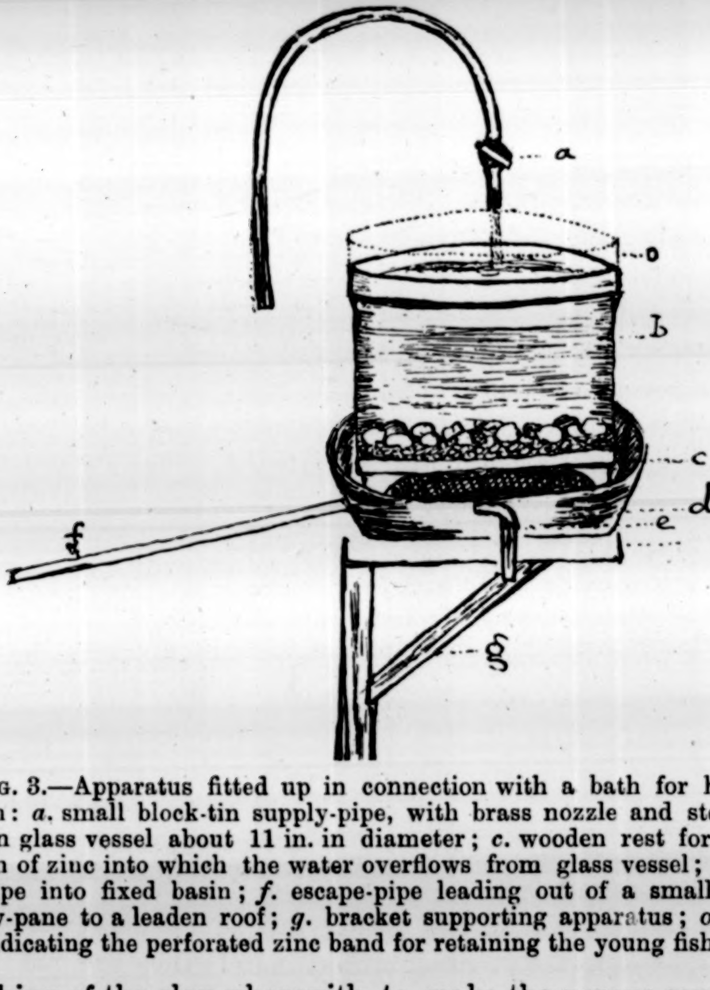


FIG. 3.—Apparatus fitted up in connection with a bath for hatching Salmon: *a*. small block-tin supply-pipe, with brass nozzle and stop-cock; *b*. green glass vessel about 11 in. in diameter; *c*. wooden rest for vessel; *d*. basin of zinc into which the water overflows from glass vessel; *e*. overflow pipe into fixed basin; *f*. escape-pipe leading out of a small hole in window-pane to a leaden roof; *g*. bracket supporting apparatus; *o*. dotted lines indicating the perforated zinc band for retaining the young fishes.

furnishing of the clay wherewith to make the porous sandy soil of the ponds impermeable. There is ample ground for extension, and the supply of pure water from Stormontfield mill-lade above them is abundant. These features have subsequently been taken advantage of by considerable additions since the period mentioned.

In a space 72 ft. square 300 wooden boxes are placed in twenty-five rows, each containing twelve boxes, on a gentle slope. In the bottom of each is placed a layer of fine gravel, with an upper loose coating of larger stones. A full supply of water is brought from the mill-lade just mentioned by a sluice and pipe, so that it bubbles up through a thick layer of sand and gravel in the filtering pond, whilst on each side of the aperture of exit is a wooden trough for collecting superfluous mud. The sole inhabitants of this pond are Minnows and Eels. From the filtering-pond the water passes by two wide pipes to the northern canal which laves the upper end of the breeding-boxes, bubbling up at the fourth box from each end, the water then rushing into each of the wide notches at the ends of the twenty-five boxes, streams longitudinally through, passing on to the next, and finally plunging from the last into the lower canal at the southern end of the boxes. A double sluice at the western corner of this canal carries the stream to the large rearing-pond further down the slope.

The gravel and stones in the boxes are carefully cleaned before collecting the ova during the spawning season, which usually is between the middle of November and the middle of December; the Salmon being captured near the mouth of the river Almond as it joins the Tay. The Salmon are gently held, and the hand passed from before backward along the belly, when the ripe ova or milt pass out by the genital aperture and drop into a vessel and then the fishes are returned to the river.* Fertilization being effected, the ova are removed to Stormont-field the same evening. It was found in 1859 that the milt of a Parr twenty months old was equally effective with that of an adult male, and no difference was observed in the growth or aspect of the young fishes subsequently reared.

Having reached the hatching-boxes, the fisherman in charge commences at one side of the rows and literally sows the ova

* This method of dealing with ripe fishes should be borne in mind. On one occasion an expert and an official were greatly perturbed as to certain ripe Turbot which would not discharge their eggs and milt; yet it was only necessary to capture the fishes with a hand-net, gently manipulate the abdomen, and a stream of ripe eggs issued at once, and were fertilized by milt from the males.

gently into each, and if they should appear too much exposed, by waving his hand in the water they readily sink under cover of the larger stones as if by instinct. The labour for a time is now over, and the water-supply of the boxes alone requires attention.

During severe winters various precautions are necessary; thus the ice on the mill-lade may block the current to the filtering-pond, and boards and straw may be required to protect the hatching-boxes from consolidation, which, in the case of the pelagic eggs of marine fishes in a tank, is so fatal. The fisherman feared that similar effects would ensue in the instance of the ova of the Salmon, but actual experiments cannot at this date be recalled. Moreover, a flock of ducks has been known during severe weather to devour all the eggs they could secure —just as Scoters and other forms at sea people a long line of floating organisms and greedily swallow the pelagic eggs of fishes.

Toward the middle of January the eyes of the embryos are visible, and about the 8th of April the earliest are hatched, the larvæ with the large yolk-sac keeping the protection of the stones in the boxes. Those which, after struggling inside the transparent capsule, emerge head first, with a few wriggles shake off the capsule and are free, represent the normal births. On the other hand, those which emerge with the tail first are less fortunate, for the egg-capsule clings round the yolk-sac and the head, and may cause the death of the young fish. In mild winters hatching occurs about thirty days sooner than in a severe one.

At this stage the little Salmon is in a rather helpless condition, though its mouth is open and it is capable of wriggling, and in its native rivers must be liable to many mishaps from spates in the mud, predatory birds, fishes and invertebrates. In the boxes they remain quiescent for six weeks longer until the large yolk-sac is absorbed, and then the tiny Parr * swim freely; and, passing the small rapids from box to box, reach the lower canal, where they do not stay long, but voluntarily seek the larger pond below by the streamlets. In the rearing-pond they are fed chiefly on boiled liver, besides such food as they can obtain amidst the water and water-plants. Next year,

* Parr are readily distinguished by the bold pigment-bars along the sides.

about the middle of May, those which become Smolts are restless and sportive, even leaping out of the pond in their endeavour to reach the river. The sluice at the east corner of the rearing-pond is then left open, and those so inclined pass down a wooden aqueduct to a small enclosure with perforated zinc, close to the river, and congregate there overnight. They are then marked by cutting off the adipose fin, and liberated into the Tay. Other methods of marking formerly adopted were "punching" out a triangular portion of the operculum, and putting rings in fins (the present method) and tail. Those which exhibit the migratory instinct generally show the silvery hue of the Smolt, and very few Parr find their way into the "trap." The rest of the young fishes remain for another year before assuming the silvery coating of the Smolt and the migratory instinct. There is thus a marked difference between such and the Pacific Salmon which passes to the sea shortly after absorption of the yolk-sac. Its scale, Dr. Masterman points out, is devoid of the primitive annular ridges.

The little fish of about an inch in length (Parr) feeds readily on minute organisms, such as copepods, in the water, gradually gains strength to encounter the currents, and at the end of the first year is about 2½–3 in. long, a few reared at Stormontfield being larger and assuming the silvery dress of the Smolt (about eight per cent.), these manifesting a desire to migrate to the river.

In the early sixties of last century the sight from the margin of the pond in August, when the vegetation had recovered from the annual clearing, was both interesting and beautiful, and the same remarks will equally apply to the present time. The bright green pond-weeds had spread in truly tropical luxuriance, transforming the pond into an enchanting sub-aqueous forest, under the shade of which the Parr, together with shoals of the three-spined Stickleback, found both shelter and food; whilst, on a lower level, numerous Loaches and a few Eels shared the same retreat. Threading their way through the sub-aqueous thickets the little Salmon keep in companies, rising readily to artificial food in good weather, or hunt the minute animals which swarmed on all sides. Larvæ of insects climbed the pond-weeds or formed their tubes on the stones. Pond-snails

glided over the sand, glistened on the stones, or fringed the green branches with their multitudes; whilst the *Confervæ* afforded lurking places for Water-beetles, Cyprides, Leeches, Worms and other invertebrates which preyed on the more minute infusoria, diatoms, and desmids. From the platform on the southern side, indeed, the sight of all this natural beauty and luxuriance, as well as the shoals of sportive fishes, involuntarily recalled the coral reefs of the South Pacific, with their gaily tinted polyps and the brightly coloured fishes which frequented them.

Since the foregoing period a new rearing-ground has been made and trees planted by the border; and it is a noteworthy feature that the young fishes thrive best in the pond fringed by the young trees—apparently since insect-life has thus been materially increased.

At the end of the second year most become Smolts, assume the silvery dress and migrate to the sea, apparently passing at once to deep water, for very few small examples (7 in.) have been captured.

It is in the sea that the Salmon obtains the abundant and rich nourishment (Herrings, Sand Eels, &c.) which enables it to increase rapidly in length and weight; so that next year it returns to its native river as a Grilse of 2–5 or more pounds; or if it remains a year longer it enters the river as a small Salmon in spring. Similar results were obtained by marking Kelts, or spent fishes, the short and the long sojourns in the sea in Scotland being respectively five months and fifteen and three-quarter months.

Its food in the sea was long a source of dubiety. Thus Knox, Huxley, Queckett and others thought that it fed on the eggs of various kinds of Echinodermata, small crustacea, and Sand Eels, apparently linking on the colour of the food with that of the muscle of the Salmon.

The Salmon is a type of a fish having demersal eggs—that is, they are deposited on the bottom; and in such fishes the eggs, while they are far larger in size, are less numerous than in those having floating or pelagic eggs. Thus the Salmon has about 28,000 eggs, the Cod from three to nine millions. The young of the Salmon is not only much larger than in the case

of pelagic eggs, its mouth is open at its birth, and its store of yolk is sufficient to nourish it for five or six weeks; whereas the young hatched from a pelagic egg, as a rule, is devoid of a mouth, has a small quantity of yolk, which in the Cod lasts only nine days, and is a minute transparent speck scarcely visible in the water except for the shimmer it makes when moving. It has at first no definite circulation, whereas the young Salmon has on its first day a most complex and complete series of arteries and veins.

The Wolf-Fish, amongst marine fishes perhaps, most nearly approaches the Salmon in the demersal condition of its eggs and in their comparatively large size, but it differs in having oviducts to convey the eggs to the exterior, and in the fact that the eggs are firmly agglutinated into a mass, and contain a single large oil-globule. The fishes on hatching are readily distinguished thus :—

	Wolf-Fish.	*Salmon.*
1.	Yolk, and contained oil-globule of inconspicuous colour, and yolk-sac spheroidal.	Yolk of reddish orange colour, and elongated in outline.
2.	Single large oil-globule, anterior in position.	Many small oil-globules in upper part of yolk-sac.
3.	Snout blunt, so that eyes at the most anterior part of head.	Snout protrudes well in front of eyes.
4.	Marginal fin continuous.	Marginal fin forming separate median fins.

Neither the Wolf-Fish nor the Salmon pays the slightest attention to its eggs after deposition, and thus they form a contrast with the next species, *viz.* the Lump-Sucker (155,000 eggs). In this form the eggs in the ovaries agree with those of the two former fishes in ripening nearly simultaneously, and they form large amethystine masses attached to the rocks between tide-marks; but, instead of being forsaken after deposition, they are jealously guarded by the male, a smaller and more brightly-coloured fish than the female. So faithfully does the male discharge this duty that at extreme low water it may happen that most of his body is exposed, so that carrion crows destroy the eyes and even puncture the abdomen for the liver of the resolute guardian.

The Gunnel is about as careful of its eggs as the foregoing,

though they are comparatively few in number, for it deposits them, as Mr. Holt found at St. Andrews, in holes (such as a large burrow of *Pholas crispata*), and the parent coils her ribbon-like body around them, after the manner of a Boa.

Space would fail, however, if the details of those having demersal eggs were entered into at length, for they are numerous, ranging from the Sea-Scorpion (*Cottus*) with its roseate masses of eggs, the Gobies with their separate eggs fixed by an elegantly reticulated series of strands, the disc-shaped eggs of the Bimaculated Sucker, the globular eggs of the Shanny with their soft adhesive rims; the golden eggs of the Armed Bull-head, the greenish yellow eggs of the Sand-Eel, and of the curious eggs of the Garfish and Saury Pike, with their external filaments resembling magnified *Globigerinæ* surrounded by their protoplasmic filaments. Yet there is one demersal form which cannot be passed by—*viz.* the Herring (25,000 eggs), which has a small egg with a tough capsule glued to its neighbours, so as to form masses adhering to a gravelly bottom in countless myriads and covering, it may be, square miles. As the Herring is often captured at the spawning season, the eggs adhere to the nets and ropes and form a coating on the deck of the boats, but so hardy and firm are they that after sixteen hours' exposure to the air they are readily hatched. Moreover, it is a curious check to theories concerning the safety of fishes having pelagic eggs to find that here is a fish, the vast multitudes of which surpass every other produced from a demersal egg, and which as time rolls on, and as methods of capture increase in intensity, seems by its undiminished shoals to set man's influence at defiance. Yet its closely related brethren, the Sprat, Pilchard, and Anchovy all have pelagic eggs, and the countless masses of the former sometimes vie with those of the Herring; indeed, as a fragment of the captures in the Forth, seventeen truckloads have been sent in a day to the Carse of Gowrie to be utilized as manure. Truly the country has not hitherto utilized all its marine sources of food-supply.

But some fishes exhibit great ingenuity by fashioning nests for the protection of their eggs—such as the 2-, 3-, and 15-spined Sticklebacks—and, moreover, they jealously guard them. The Gourami of the Malay Archipelago (*Osphromenus gouramy*)

makes a nest of floating weeds and attaches it to other water-plants; others, such as *Macropodus* (Paradise Fish), use the buccal secretion and air bubbles to float it, and in both cases keep guard over the eggs. Many of the *Centrarchidæ* (the group which contains the Black Bass) make nests, and so with the American *Amiurus nebulosus* (a Cat-Fish), and in the latter case the male guards. *Doras*, *Corydoras* and *Callichthys* of South America make nests of grass and leaves, and both male and female guard. *Gymnarchus* of the Gambia constructs a floating nest and the male guards; whilst *Heterotis niloticus* makes enormous nests in the swamps of the same region. The curious little *Antennarius* fashions a nest of the floating *Sargassum*, fixing, by aid of the same secretion as in the 15-spined Stickleback, the weeds to protect the eggs—which are like bunches of grapes.

Still more curious is the habit of *Rhodeus amarus*, the Bitterling of Europe (allied to the Dace, Chub, and Minnow), the female of which with its long ovipositor inserts the eggs into the mantle-cavities of *Unio* or *Anodon*, where they are duly hatched and reared. *Aspredo platystacus* (a Cat-Fish), however, is a better nurse, since the female attaches the eggs to the spongy papillose surface of the abdomen; and so are the males of the Pipe-Fishes, which carry the eggs in a long groove or pouch on the under surface. Moreover, as if to demonstrate the illimitability of Nature's resources, the mouth and pharynx are used as brood-pouches in the male Siluroids *Arius*, *Galeichthys*, and in the male *Osteogenissus*, the females more rarely performing the same functions; and in *Arius commersonii* the eggs are from 17–18 mm. in diameter. No food occurred in the stomachs of those in this condition.* *Malapterurus*, again, is said to shelter its fry in its mouth. But these do not exhaust the remarkable variations met with in Teleostean reproduction, for not a few are viviparous. Thus in our own country the viviparous Blenny is a familiar instance, with its large young; and the Norway Haddock is another less common form, with its small embryos. Abroad, the viviparous forms range from Mud-Minnows

* A vertebrate parallel to the condition of *Asterias mülleri* in the rock-pools at St. Andrews, the female of which carries a mass of ova over the mouth.

(*Umbridæ*), Killi-Fishes (Cyprinodonts), in which the anal fin is modified into a long intermittent organ in the male, to Surf-Fishes (*Embiotocidæ–Labyrinthieci*), such as the White Surf-Fish (*Cymatogaster aggregatus*) with very large young. Even the blind Brotula (*Lucifuga subterranea*) of Cuba, one of the Blennies, is in this condition.

Whilst the previous methods of reproduction are both important and interesting, they hold but a minor position when contrasted with the striking and far-reaching influence of the discharge of pelagic eggs—a method so prevalent in the marine food-fishes; for, strange to say, almost the entire series comes under this category—only the Herring, the Wolf-Fish, and the Norway Haddock being the exceptions. It is this pelagic condition of the vast swarms of the minute eggs which has preserved these valuable fishes from serious diminution by man, whose fishing apparatus—often on a gigantic scale—searches the seas in every clime and especially in the much-frequented North Sea and the coasts of Europe, the American shores, those of Asia, Africa, Japan, Australia and New Zealand. Fears, it is true, are ever present with those whose scientific knowledge of the subject is limited, and new methods of fishing have not always been welcome, yet both conditions have existed for many centuries and will, in all probability, continue. Some may remember the general clamour on the introduction of steam-trawling into Scottish waters, and the resolute opposition it met with on every side from members of Parliament to line- and net-fishermen, yet in some instances the same method had been practised by the liners in their sailing boats for many years, and it was only the appearance of powerful steam vessels to compete with them in their own areas which roused opposition. Yet, after all, there is little difference, for instance, between capturing tons of Plaice by aid of hundreds of nets hung thickly throughout a bay, and sweeping them from the bottom by either beam or other trawl; indeed, many adult Plaice escape the two latter by sinking in the sand. But capture persistently as man may, the pelagic eggs and larvæ spread each species widely over the sea, many by-and-by having a definite drift as larval or post-larval forms—irrespective of those diverse currents, salinities and temperature of which we hear so much from recent investiga-

tors. Hydrographically, all these observations are of great interest and merit respect, but as an international method of solving the fisheries' problems they have not been a success. It is fruitless to ask these to explain why the larval and young Plaice year after year invariably seek the margin of the sandy beach, why the young Cod keeps to deep water till it is an inch in length and then comes to the margin of the rocks, going out again as it gets older, why the young Haddock, on the other hand, remains in deep water till it is four to five inches in length, when it passes to the inshore waters. The laws that guide these and similar cases are beyond the influences of currents, temperatures, or salinities.

The international investigators, who promised results of importance within two years, after fully eleven years' labours have at last narrowed and focussed their recommendations to the protection of the Plaice, chiefly by a size limit, an idea long known, and indeed put in force by certain nations about a quarter of a century ago; this and the *camaraderie* of the fisheries' representatives, scientific and otherwise, is perhaps the main result of an expenditure of more than £100,000 by our own country! Yet it is only fair to add that the Danish ship, with Dr. Johs. Schmidt on board, has notably extended our knowledge of the life-history of the Common Eel which spawns only in mid-Atlantic, the young thereafter traversing the entire length of the Mediterranean, besides supplying the whole of the western border of Europe.

A calm survey of the reproduction of fishes thus opens up a vast field for reflection, and impresses the observer at once with the illimitability of Nature's resources and the fine adjustment in every case to the needs of the species. Whether conditions so remarkable were the result of gradual evolution or formed by more or less sudden leaps has not been fully investigated. Yet there cannot be a doubt that through all the mazes of those wonderful complexities a Master Mind has ruled what was best for each, so that not one of the recent species has failed to preserve its existence under the most diverse circumstances, and with the increasing drain on its numbers by the cupidity of man.

BRITISH ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE, AUSTRALIA, 1914.

ADDRESS BY PROFESSOR WILLIAM BATESON, M.A., F.R.S., *President*.

PART I.—MELBOURNE.

THE outstanding feature of this Meeting must be the fact that we are here—in Australia. It is the function of a President to tell the Association of advances in science, to speak of the universal rather than of the particular or the temporary. There will be other opportunities of expressing the thoughts which this event must excite in the dullest heart, but it is right that my first words should take account of those achievements of organisation and those acts of national generosity by which it has come to pass that we are assembled in this country. Let us, too, on this occasion, remember that all the effort, and all the goodwill, that binds Australia to Britain would have been powerless to bring about such a result had it not been for those advances in science which have given man a control of the forces of Nature. For we are here by virtue of the feats of genius of individual men of science, giant-variations from the common level of our species; and since I am going soon to speak of the significance of individual variation, I cannot introduce that subject better than by calling to remembrance the line of pioneers in chemistry, in physics, and in engineering, by the working of whose rare—or, if you will, abnormal—intellects a meeting of the British Association on this side of the globe has been made physically possible.

I have next to refer to the loss within the year of Sir David Gill, a former President of this Association, himself one of the outstanding great. His greatness lay in the power of making big foundations. He built up the Cape Observatory, he organised international geodesy; he conceived and carried through the plans for the photography of the whole sky, a work in which Australia is bearing a conspicuous part. Astronomical observation is now organised on an international scale, and of this great scheme Gill was the heart and soul. His labours have ensured a base from which others will proceed to discovery otherwise impossible. His name will be long remembered with veneration and gratitude.

As the subject of the addresses which I am to deliver here and in Sydney I take Heredity. I shall attempt to give the essence of the discoveries made by Mendelian or analytical methods of study, and I shall ask you to contemplate the deductions which these physiological facts suggest in application both to evolutionary theory at large and to the special case of the natural history of human society.

Recognition of the significance of heredity is modern. The term itself in its scientific sense is no older than Herbert Spencer. Animals

and plants are formed as pieces of living material split from the body of the parent organisms. Their powers and faculties are fixed in their physiological origin. They are the consequence of a genetic process, and yet it is only lately that this genetic process has become the subject of systematic research and experiment. The curiosity of naturalists has of course always been attracted to such problems; but that accurate knowlege of genetics is of paramount importance in any attempt to understand the nature of living things has only been realised quite lately even by naturalists, and with casual exceptions the laity still know nothing of the matter. Historians debate the past of the human species, and statesmen order its present or profess to guide its future as if the animal Man, the unit of their calculations, with his vast diversity of powers, were a homogeneous material, which can be multiplied like shot.

The reason for this neglect lies in ignorance and misunderstanding of the nature of Variation; for not until the fact of congenital diversity is grasped, with all that it imports, does knowledge of the system of hereditary transmission stand out as a primary necessity in the construction of any theory of Evolution, or any scheme of human polity.

The first full perception of the significance of variation we owe to Darwin. The present generation of evolutionists realises perhaps more fully than did the scientific world in the last century that the theory of evolution had occupied the thoughts of many and found acceptance with not a few before ever the 'Origin' appeared. We have come also to the conviction that the principle of Natural Selection cannot have been the chief factor in delimiting the species of animals and plants, such as we now with fuller knowledge see them actually to be. We are even more sceptical as to the validity of that appeal to changes in the conditions of life as direct causes of modification, upon which latterly at all events Darwin laid much emphasis. But that he was the first to provide a body of fact demonstrating the variability of living things, whatever be its causation, can never be questioned.

There are some older collections of evidence, chiefly the work of the French school, especially of Godron *—and I would mention also the almost forgotten essay of Wollaston †—these, however, are only fragments in comparison. Darwin regarded variability as a property inherent in living things, and eventually we must consider whether this conception is well founded; but postponing that inquiry for the present, we may declare that with him began a general recognition of variation as a phenomenon widely occurring in Nature.

If a population consists of members which are not alike but differentiated, how will their characteristics be distributed among their offspring? This is the problem which the modern student of heredity sets out to investigate. Formerly it was hoped that by the simple inspection of embryological processes the modes of heredity

* 'De l'Espèce et des Races dans les Êtres Organisés,' 1859.
† 'On the Variation of Species,' 1856.

might be ascertained, the actual mechanism by which the offspring is formed from the body of the parent. In that endeavour a noble pile of evidence has been accumulated. All that can be made visible by existing methods has been seen, but we come little, if at all, nearer to the central mystery. We see nothing that we can analyse further—nothing that can be translated into terms less inscrutable than the physiological events themselves. Not only does embryology give no direct aid, but the failure of cytology is, so far as I can judge, equally complete. The chromosomes of nearly related creatures may be utterly different both in number, size, and form. Only one piece of evidence encourages the old hope that a connection might be traceable between the visible characteristics of the body and those of the chromosomes. I refer of course to the accessory chromosome, which in many animals distinguishes the spermatozoon about to form a female in fertilization. Even it, however, cannot be claimed as the cause of sexual differentiation, for it may be paired in forms closely allied to those in which it is unpaired or accessory. The distinction may be present or wanting, like any other secondary sexual character. Indeed, so long as no one can show consistent distinctions between the cytological characters of somatic tissues in the same individual we can scarcely expect to perceive such distinctions between the chromosomes of the various types.

For these methods of attack we now substitute another, less ambitious, perhaps, because less comprehensive, but not less direct. If we cannot see how a fowl by its egg and its sperm gives rise to a chicken or how a Sweet Pea from its ovule and its pollen grain produces another Sweet Pea, we at least can watch the system by which the differences between the various kinds of fowls or between the various kinds of Sweet Peas are distributed among the offspring. By thus breaking the main problem up into its parts we give ourselves fresh chances. This analytical study we call Mendelian, because Mendel was the first to apply it. To be sure, he did not approach the problem by any such line of reasoning as I have sketched. His object was to determine the genetic definiteness of species; but though in his writings he makes no mention of inheritance it is clear that he had the extension in view. By crossbreeding he combined the characters of varieties in mongrel individuals, and set himself to see how these characters would be distributed among the individuals of subsequent generations. Until he began this analysis nothing but the vaguest answers to such a question had been attempted. The existence of any orderly system of descent was never even suspected. In their manifold complexity human characteristics seemed to follow no obvious system, and the fact was taken as a fair sample of the working of heredity.

Misconception was especially brought in by describing descent in terms of "blood." The common speech uses expressions such as consanguinity, pure-blooded, half-blood, and the like, which call up a misleading picture to the mind. Blood is in some respects a fluid, and thus it is supposed that this fluid can be both quantitatively and qualitatively diluted with other bloods, just as treacle can be diluted

with water. Blood in primitive physiology being the peculiar vehicle of life, at once its essence and its corporeal abode, these ideas of dilution and compounding of characters in the commingling of bloods inevitably suggest that the ingredients of the mixture once combined are inseparable, that they can be brought together in any relative amounts, and in short that in heredity we are concerned mainly with a quantitative problem. Truer notions of genetic physiology are given by the Hebrew expression "seed." If we speak of a man as "of the blood-royal" we think at once of plebeian dilution, and we wonder how much of the royal fluid is likely to be "in his veins"; but if we say he is "of the seed of Abraham" we feel something of the permanence and indestructibility of that germ which can be divided and scattered among all nations, but remains recognisable in type and characteristics after 4000 years.

I knew a breeder who had a chest containing bottles of coloured liquids by which he used to illustrate the relationships of his dogs, pouring from one to another and titrating them quantitatively to illustrate their pedigrees. Galton was beset by the same kind of mistake when he promulgated his "Law of Ancestral Heredity." With modern research all this has been cleared away. The allotment of characteristics among offspring is not accomplished by the exudation of drops of a tincture representing the sum of the characteristics of the parent organism, but by a process of cell-division, in which numbers of these characters, or rather the elements upon which they depend, are sorted out among the resulting germ-cells in an orderly fashion. What these elements, or factors as we call them, are we do not know. That they are in some way directly transmitted by the material of the ovum and of the spermatozoon is obvious, but it seems to me unlikely that they are in any simple or literal sense material particles. I suspect rather that their properties depend on some phenomenon of arrangement. However that may be, analytical breeding proves that it is according to the distribution of these genetic factors, to use a non-committal term, that the characters of the offspring are decided. The first business of experimental genetics is to determine their number and interactions, and then to make an analysis of the various types of life.

Now the ordinary genealogical trees, such as those which the stud-books provide in the case of the domestic animals, or the Heralds' College provides in the case of man, tell nothing of all this. Such methods of depicting descent cannot even show the one thing they are devised to show—purity of "blood." For at last we know the physiological meaning of that expression. An organism is pure-bred when it has been formed by the union in fertilization of two germ-cells which are alike in the factors they bear; and since the factors for the several characteristics are independent of each other, this question of purity must be separately considered for each of them. A man, for example, may be pure-bred in respect of his musical ability and cross-bred in respect of the colour of his eyes or the shape of his mouth. Though we know nothing of the essential nature of these factors, we know a good deal of their powers. They

may confer height, colour, shape, instincts, powers both of mind and body; indeed, so many of the attributes which animals and plants possess that we feel justified in the expectation that with continued analysis they will be proved to be responsible for most if not all of the differences by which the varying individuals of any species are distinguished from each other. I will not assert that the greater differences which characterize distinct species are due generally to such independent factors, but that is the conclusion to which the available evidence points. All this is now so well understood, and has been so often demonstrated and expounded, that details of evidence are now superfluous.

But for the benefit of those who are unfamiliar with such work let me briefly epitomise its main features and consequences. Since genetic factors are definite things, either present in or absent from any germ-cell, the individual may be either "pure-bred" for any particular factor, or its absence, if he is constituted by the union of two germ-cells both possessing or both destitute of that factor. If the individual is thus pure, all his germ-cells will in that respect be identical, for they are simply bits of the similar germ-cells which united in fertilization to produce the parent organism. We thus reach the essential principle, that an organism cannot pass on to offspring a factor which it did not itself receive in fertilization. Parents, therefore, which are both destitute of a given factor can only produce offspring equally destitute of it; and, on the contrary, parents both pure-bred for the presence of a factor produce offspring equally pure-bred for its presence. Whereas the germ-cells of the pure-bred are all alike, those of the cross-bred, which results from the union of dissimilar germ-cells, are mixed in character. Each positive factor segregates from its negative opposite, so that some germ-cells carry the factor and some do not. Once the factors have been identified by their effects, the average composition of the several kinds of families formed from the various matings can be predicted.

Only those who have themselves witnessed the fixed operations of these simple rules can feel their full significance. We come to look behind the simulacrum of the individual body, and we endeavour to disintegrate its features into the genetic elements by whose union the body was formed. Set out in cold general phrases such discoveries may seem remote from ordinary life. Become familiar with them and you will find your outlook on the world has changed. Watch the effects of segregation among the living things with which you have to do—Plants, Fowls, Dogs, Horses, that mixed concourse of humanity we call the English race, your friends' children, your own children, yourself—and however firmly imagination be restrained to the bounds of the known and the proved, you will feel something of that range of insight into nature which Mendelism has begun to give. The question is often asked whether there are not also in operation systems of descent quite other than those contemplated by the Mendelian rules. I myself have expected such discoveries, but hitherto none have been plainly demonstrated. It is true we are often puzzled by the

failure of a parental type to reappear in its completeness after a cross—the merino sheep or the fantail pigeon, for example. These exceptions may still be plausibly ascribed to the interference of a multitude of factors, a suggestion not easy to disprove; though it seems to me equally likely that segregation has been in reality imperfect. Of the descent of quantitative characters we still know practically nothing. These and hosts of difficult cases remain almost untouched. In particular the discovery of E. Baur, and the evidence of Winkler in regard to his "graft hybrids," both showing that the sub-epidermal layer of a plant—the layer from which the germ-cells are derived—may bear exclusively the characters of a part only of the soma, give hints of curious complications, and suggest that in plants at least the interrelations between soma and gamete may be far less simple than we have supposed. Nevertheless, speaking generally, we see nothing to indicate that qualitative characters descend, whether in plants or animals, according to systems which are incapable of factorial representation.

The body of evidence accumulated by this method of analysis is now very large, and is still growing fast by the labours of many workers. Progress is also beginning along many novel and curious lines. The details are too technical for inclusion here. Suffice it to say that not only have we proof that segregation affects a vast range of characteristics, but in the course of our analysis phenomena of most unexpected kinds have been encountered. Some of these things twenty years ago must have seemed inconceivable. For example, the two sets of sex organs, male and female, of the same plant may not be carrying the same characteristics; in some animals characteristics, quite independent of sex, may be distributed solely or predominantly to one sex; in certain species the male may be breeding true to its own type, while the female is permanently mongrel, throwing off eggs of a distinct variety in addition to those of its own type; characteristics, essentially independent, may be associated in special combinations which are largely retained in the next generation, so that among the grandchildren there is numerical preponderance of those combinations which existed in the grandparents—a discovery which introduces us to a new phenomenon of polarity in the organism.

We are accustomed to the fact that the fertilised egg has a polarity, a front and hind end for example; but we have now to recognise that it, or the primitive germinal cells formed from it, may have another polarity shown in the groupings of the parental elements. I am entirely sceptical as to the occurrence of segregation solely in the maturation of the germ-cells,* preferring at present to regard it as a special case of that patch-work condition we see in so many plants. These mosaics may break up, emitting bud-sports at various cell-divisions, and I suspect that the great regularity seen in the F_2 ratios of the cereals, for example, is a consequence of very late segregation, whereas the excessive irregularity found in other cases

* The fact that in certain plants the male and female organs respectively carry distinct factors may be quoted as almost decisively negativing the suggestion that segregation is confined to the reduction division.

may be taken to indicate that segregation can happen at earlier stages of differentiation.

The paradoxical descent of colour-blindness and other sex-limited conditions—formerly regarded as an inscrutable caprice of nature—has been represented with approximate correctness, and we already know something as to the way, or, perhaps, I should say ways, in which the determination of sex is accomplished in some of the forms of life—though, I hasten to add, we have no inkling as to any method by which that determination may be influenced or directed. It is obvious that such discoveries have bearings on most of the problems, whether theoretical or practical, in which animals and plants are concerned. Permanence or change of type, perfection of type, purity or mixture of race, "racial development," the succession of forms, from being vague phrases expressing matters of degree, are now seen to be capable of acquiring physiological meanings, already to some extent assigned with precision. For the naturalist—and it is to him that I am especially addressing myself to-day—these things are chiefly significant as relating to the history of organic beings—the theory of Evolution, to use our modern name. They have, as I shall endeavour to show in my second address to be given in Sydney, an immediate reference to the conduct of human society.

I suppose that everyone is familiar in outline with the theory of the Origin of Species which Darwin promulgated. Through the last fifty years this theme of the Natural Selection of favoured races has been developed and expounded in writings innumerable. Favoured races certainly can replace others. The argument is sound, but we are doubtful of its value. For us that debate stands adjourned. We go to Darwin for his incomparable collection of facts. We would fain emulate his scholarship, his width and his power of exposition, but to us he speaks no more with philosophical authority. We read his scheme of Evolution as we would those of Lucretius or of Lamarck, delighting in their simplicity and their courage. The practical and experimental study of Variation and Heredity has not merely opened a new field; it has given a new point of view and new standards of criticism. Naturalists may still be found expounding teleological systems* which would have delighted Dr. Pangloss

* I take the following from the Abstract of a recent Croonian Lecture "On the Origin of Mammals" delivered to the Royal Society:—"In Upper Triassic times the larger Cynodonts preyed upon the large Anomodont, *Kannemeyeria*, and carried on their existence so long as these Anomodonts survived, but died out with them about the end of the Trias or in Rhætic times. The small Cynodonts, having neither small Anomodonts nor small Cotylosaurs to feed on, were forced to hunt the very active long-limbed Thecodonts. The greatly increased activity brought about that series of changes which formed the mammals—the flexible skin with hair, the four-chambered heart and warm blood, the loose jaw with teeth for mastication, an increased development of tactile sensation and a great increase of cerebrum. Not improbably the attacks of the newly-evolved Cynodont or mammalian type brought about a corresponding evolution in the Pseudosuchian Thecodonts which ultimately resulted in the formation of Dinosaurs and Birds." Broom, R., Proc. Roy. Soc. B., 87, p. 88.

himself, but at the present time few are misled. The student of genetics knows that the time for the development of theory is not yet. He would rather stick to the seed-pan and the incubator.

In face of what we now know of the distribution of variability in nature the scope claimed for Natural Selection in determining the fixity of species must be greatly reduced. The doctrine of the survival of the fittest is undeniable so long as it is applied to the organism as a whole, but to attempt by this principle to find value in all definiteness of parts and functions, and in the name of Science to see fitness everywhere is mere eighteenth-century optimism. Yet it was in application to the parts, to the details of specific difference, to the spots on the Peacock's tail, to the colouring of an Orchid flower, and hosts of such examples, that the potency of Natural Selection was urged with the strongest emphasis. Shorn of these pretensions the doctrine of the survival of favoured races is a truism, helping scarcely at all to account for the diversity of species. Tolerance plays almost as considerable a part. By these admissions almost the last shred of that teleological fustian with which Victorian philosophy loved to clothe the theory of Evolution is destroyed. Those who would proclaim that whatever is is right will be wise henceforth to base this faith frankly on the impregnable rock of superstition and to abstain from direct appeals to natural fact.

My predecessor said last year that in physics the age is one of rapid progress and profound scepticism. In at least as high a degree this is true of Biology, and as a chief characteristic of modern evolutionary thought we must confess also to a deep but irksome humility in presence of great vital problems. Every theory of Evolution must be such as to accord with the facts of physics and chemistry, a primary necessity to which our predecessors paid small heed. For them the unknown was a rich mine of possibilities on which they could freely draw. For us it is rather an impenetrable mountain out of which the truth can be chipped in rare and isolated fragments. Of the physics and chemistry of life we know next to nothing. Somehow the characters of living things are bound up in properties of colloids, and are largely determined by the chemical powers of enzymes, but the study of these classes of matter have only just begun. Living things are found by a simple experiment to have powers undreamt of, and who knows what may be behind?

Naturally we turn aside from generalities. It is no time to discuss the origin of the Mollusca or of Dicotyledons, while we are not even sure how it came to pass that *Primula obconica* has in twenty-five years produced its abundant new forms almost under our eyes. Knowledge of heredity has so reacted on our conceptions of variation that very competent men are even denying that variation in the old sense is a genuine occurrence at all. Variation is postulated as the basis of all evolutionary change. Do we then as a matter of fact find in the world about us variations occurring of such a kind as to warrant faith in a contemporary progressive Evolution? Till lately most of us would have said "yes" without misgiving. We should have pointed, as Darwin did, to the immense

range of diversity seen in many wild species, so commonly that the difficulty is to define the types themselves. Still more conclusive seemed the profusion of forms in the various domesticated animals and plants, most of them incapable of existing even for a generation in the wild state, and therefore fixed unquestionably by human selection. These, at least, for certain, are new forms, often distinct enough to pass for species, which have arisen by variation. But when analysis is applied to this mass of variation the matter wears a different aspect. Closely examined, what is the "variability" of wild species? What is the natural fact which is denoted by the statement that a given species exhibits much variation? Generally one of two things: either that the individuals collected in one locality differ among themselves; or perhaps more often that samples from separate localities differ from each other. As direct evidence of variation it is clearly to the first of these phenomena that we must have recourse—the heterogeneity of a population breeding together in one area. This heterogeneity may be in any degree, ranging from slight differences that systematists would disregard, to a complex variability such as we find in some moths, where there is an abundance of varieties so distinct that many would be classified as specific forms but for the fact that all are freely breeding together. Naturalists formerly supposed that any of these varieties might be bred from any of the others. Just as the reader of novels is prepared to find that any kind of parents might have any kind of children in the course of the story, so was the evolutionist ready to believe that any pair of moths might produce any of the varieties included in the species. Genetic analysis has disposed of all these mistakes. We have no longer the smallest doubt that in all these examples the varieties stand in a regular descending order, and that they are simply terms in a series of combinations of factors separately transmitted, of which each may be present or absent.

The appearance of contemporary variability proves to be an illusion. Variation from step to step in the series must occur either by the addition or by the loss of a factor. Now, of the origin of new forms *by loss* there seems to me to be fairly clear evidence, but of the *contemporary acquisition* of any new factor I see no satisfactory proof, though I admit there are rare examples which may be so interpreted. We are left with a picture of variation utterly different from that which we saw at first. Variation now stands out as a definite physiological event. We have done with the notion that Darwin came latterly to favour, that large differences can arise by accumulation of small differences. Such small differences are often mere ephemeral effects of conditions of life, and as such are not transmissible; but even small differences, when truly genetic, are factorial like the larger ones, and there is not the slightest reason for supposing that they are capable of summation. As to the origin or source of these positive separable factors, we are without any indication or surmise. By their effects we know them to be definite, as definite, say, as the organisms which produce diseases; but how they arise and how they come to take part in the composition of the

living creature so that when present they are treated in cell-division as constituents of the germs, we cannot conjecture.

It was a commonplace of evolutionary theory that at least the domestic animals have been developed from a few wild types. Their origin was supposed to present no difficulty. The various races of Fowl, for instance, all came from *Gallus bankiva*, the Indian Jungle-Fowl. So we are taught; but try to reconstruct the steps in their evolution and you realise your hopeless ignorance. To be sure there are breeds, such as Black-red Game and Brown Leghorns, which have the colours of the Jungle-Fowl, though they differ in shape and other respects. As we know so little as yet of the genetics of shape, let us assume that those transitions could be got over. Suppose, further, as is probable, that the absence of the maternal instinct in the Leghorn is due to loss of one factor which the Jungle-Fowl possesses. So far we are on fairly safe ground. But how about White Leghorns? Their origin may seem easy to imagine, since white varieties have often arisen in well-authenticated cases. But the white of White Leghorns is not, as white in nature often is, due to the loss of the colour-elements, but to the action of something which inhibits their expression. Whence did that something come? The same question may be asked respecting the heavy breeds, such as Malays or Indian Game. Each of these is a separate introduction from the East. To suppose that these, with their peculiar combs and close feathering, could have been developed from pre-existing European breeds is very difficult. On the other hand, there is no wild species now living any more like them. We may, of course, postulate that there was once such a species, now lost. That is quite conceivable, though the suggestion is purely speculative. I might thus go through the list of domesticated animals and plants of ancient origin and again and again we should be driven to this suggestion, that many of their distinctive characters must have been derived from some wild original now lost. Indeed, to this unsatisfying conclusion almost every careful writer on such subjects is now reduced. If we turn to modern evidence the case looks even worse. The new breeds of domestic animals made in recent times are the carefully selected products of recombination of pre-existing breeds. Most of the new varieties of cultivated plants are the outcome of deliberate crossing. There is generally no doubt in the matter. We have pretty full histories of these crosses in Gladiolus, Orchids, Cineraria, Begonia, Calceolaria, Pelargonium, &c. A very few certainly arise from a single origin. The Sweet Pea is the clearest case, and there are others which I should name with hesitation. The Cyclamen is one of them, but we know that efforts to cross Cyclamens were made early in the cultural history of the plant, and they may very well have been successful. Several plants for which single origins are alleged, such as the Chinese Primrose, the Dahlia, and Tobacco, came to us in an already domesticated state, and their origins remain altogether mysterious. Formerly single origins were generally presumed, but at the present time numbers of the chief products of domestication, Dogs, Horses, Cattle,

Sheep, Poultry, Wheat, Oats, Rice, Plums, Cherries, have in turn been accepted as "polyphyletic" or, in other words, derived from several distinct forms. The reason that has led to these judgments is that the distinctions between the chief varieties can be traced as far back as the evidence reaches, and that these distinctions are so great, so far transcending anything that we actually know variation capable of effecting, that it seems pleasanter to postpone the difficulty, relegating the critical differentiation to some misty antiquity into which we shall not be asked to penetrate. For it need scarcely be said that this is mere procrastination. If the origin of a form under domestication is hard to imagine, it becomes no easier to conceive of such enormous deviations from type coming to pass in the wild state. Examine any two thoroughly distinct species which meet each other in their distribution, as, for instance, *Lychnis diurna* and *vespertina* do. In areas of overlap are many intermediate forms. These used to be taken to be transitional steps, and the specific distinctness of *vespertina* and *diurna* was on that account questioned. Once it is known that these supposed intergrades are merely mongrels between the two species the transition from one to the other is practically beyond our powers of imagination to conceive. If both these can survive, why has their common parent perished? Why when they cross do they not reconstruct it instead of producing partially sterile hybrids? I take this example to show how entirely the facts were formerly misinterpreted.

When once the idea of a true-breeding—or, as we say, homozygous—type is grasped, the problem of variation becomes an insistent oppression. What can make such a type vary? We know, of course, one way by which novelty can be introduced—by crossing. Cross two well-marked varieties—for instance, of Chinese Primula—each breeding true, and in the second generation by mere recombination of the various factors which the two parental types severally introduced, there will be a profusion of forms, utterly unlike each other, distinct also from the original parents. Many of these can be bred true, and if found wild would certainly be described as good species. Confronted by the difficulty I have put before you, and contemplating such amazing polymorphism in the second generation from a cross in *Antirrhinum*, Lotsy has lately with great courage suggested to us that all variation may be due to such crossing. I do not disguise my sympathy with this effort. After the blind complacency of conventional evolutionists it is refreshing to meet so frank an acknowledgment of the hardness of the problem. Lotsy's utterance will at least do something to expose the artificiality of systematic zoology and botany. Whatever might or might not be revealed by experimental breeding, it is certain that without such tests we are merely guessing when we profess to distinguish specific limits and to declare that this is a species and that a variety. The only definable unit in classification is the homozygous form which breeds true. When we presume to say that such and such differences are trivial and such others valid, we are commonly embarking on a course for which there is no physiological warrant. Who could have

foreseen that the Apple and the Pear—so like each other that their botanical differences are evasive—could not be crossed together, though species of Antirrhinum so totally unlike each other as *majus* and *molle* can be hybridized, as Baur has shown, without a sign of impaired fertility? Jordan was perfectly right. The true-breeding forms which he distinguished in such multitudes are real entities, though the great systematists, dispensing with such laborious analysis, have pooled them into arbitrary Linnean species, for the convenience of collectors and for the simplification of catalogues. Such pragmatical considerations may mean much in the museum, but with them the student of the physiology of variation has nothing to do. These "little species," finely cut, true-breeding, and innumerable mongrels between them, are what he finds when he examines any so-called variable type. On analysis the semblance of variability disappears, and the illusion is shown to be due to segregation and recombination of series of factors on pre-determined lines. As soon as the "little species" are separated out they are found to be fixed. In face of such a result we may well ask with Lotsy, is there such a thing as spontaneous variation anywhere? His answer is that there is not.

Abandoning the attempt to show that positive factors can be added to the original stock, we have further to confess that we cannot often actually prove variation by loss of factor to be a real phenomenon. Lotsy doubts whether even this phenomenon occurs. The sole source of variation, in his view, is crossing. But here I think he is on unsafe ground. When a well-established variety like "Crimson King" Primula, bred by Messrs. Sutton in thousands of individuals, gives off, as it did a few years since, a salmon-coloured variety, "Coral King," we might claim this as a genuine example of variation by loss. The new variety is a simple recessive. It differs from "Crimson King" only in one respect, the loss of a single colour-factor, and, of course, bred true from its origin. To account for the appearance of such a new form by any process of crossing is exceedingly difficult. From the nature of the case there can have been no cross since "Crimson King" was established, and hence the salmon must have been concealed as a recessive from the first origin of that variety, even when it was represented by very few individuals, probably only by a single one. Surely, if any of these had been heterozygous for salmon this recessive could hardly have failed to appear during the process of self-fertilisation by which the stock would be multiplied, even though that selfing may not have been strictly carried out. Examples like this seem to me practically conclusive.* They can be challenged, but not, I think, successfully. Then again in regard to those variations in number and division of parts which we call meristic, the reference of these to original cross-breeding is surely barred by the circumstances in which they often occur. There remain also the rare examples mentioned already in

* The numerous and most interesting "mutations" recorded by Professor T. H. Morgan and his colleagues in the fly, *Drosophila*, may also be cited as unexceptionable cases.

which a single wild origin may with much confidence be assumed. In spite of repeated trials, no one has yet succeeded in crossing the Sweet Pea with any other leguminous species. We know that early in its cultivated history it produced at least two marked varieties which I can only conceive of as spontaneously arising, though, no doubt, the profusion of forms we now have was made by the crossing of those original varieties. I mention the Sweet Pea thus prominently for another reason, that it introduces us to another though subsidiary form of variation, which may be described as a *fractionation* of factors. Some of my Mendelian colleagues have spoken of genetic factors as permanent and indestructible. Relative permanence in a sense they have, for they commonly come out unchanged after segregation. But I am satisfied that they may occasionally undergo a quantitative disintegration, with the consequence that varieties are produced intermediate between the integral varieties from which they were derived. These disintegrated conditions I have spoken of as subtraction—or reduction—stages. For example, the Picotee Sweet Pea, with its purple edges, can surely be nothing but a condition produced by the factor which ordinarily makes the fully purple flower, quantitatively diminished. The pied animal, such as the Dutch Rabbit, must similarly be regarded as the result of partial defect of the chromogen from which the pigment is formed, or conceivably of the factor which effects its oxidation. On such lines I think we may with great confidence interpret all those intergrading forms which breed true and are not produced by factorial interference.

It is to be inferred that these fractional degradations are the consequence of irregularities in segregation. We constantly see irregularities in the ordinary meristic processes, and in the distribution of somatic differentiation. We are familiar with half segments, with imperfect twinning, with leaves partially petaloid, with petals partially sepaloid. All these are evidences of departures from the normal regularity in the rhythms of repetition, or in those waves of differentiation by which the qualities are sorted out among the parts of the body. Similarly, when in segregation the qualities are sorted out among the germ-cells in certain critical cell-divisions, we cannot expect these differentiating divisions to be exempt from the imperfections and irregularities which are found in all the grosser divisions that we can observe. If I am right, we shall find evidence of these irregularities in the association of unconformable numbers with the appearance of the novelties which I have called fractional. In passing, let us note how the history of the Sweet Pea belies those ideas of a continuous evolution with which we had formerly to contend. The big varieties came first. The little ones have arisen later, as I suggest by fractionation. Presented with a collection of modern Sweet Peas, how prettily would the devotees of Continuity have arranged them in a graduated series, showing how every intergrade could be found, passing from the full colour of the wild Sicilian species in one direction to white, in the other to the deep purple of "Black Prince," though happily we know these two to be among the earliest to have appeared.

Having in view these and other considerations which might be developed, I feel no reasonable doubt that though we may have to forgo a claim to variations by addition of factors, yet variation both by loss of factors and by fractionation of factors is a genuine phenomenon of contemporary nature. If then we have to dispense, as seems likely, with any addition from without we must begin seriously to consider whether the course of Evolution can at all reasonably be represented as an unpacking of an original complex which contained within itself the whole range of diversity which living things present. I do not suggest that we should come to a judgment as to what is or is not probable in these respects. As I have said already, this is no time for devising theories of Evolution, and I propound none. But as we have got to recognise that there has been an Evolution, that somehow or other the forms of life have arisen from fewer forms, we may as well see whether we are limited to the old view that evolutionary progress is from the simple to the complex, and whether after all it is conceivable that the process was the other way about. When the facts of genetic discovery became familiarly known to biologists, and cease to be the preoccupation of a few, as they still are, many and long discussions must inevitably arise on the question, and I offer these remarks to prepare the ground. I ask you simply to open your minds to this possibility. It involves a certain effort. We have to reverse our habitual modes of thought. At first it may seem rank absurdity to suppose that the primordial form or forms of protoplasm could have contained complexity enough to produce the divers types of life. But is it easier to imagine that these powers could have been conveyed by extrinsic additions? Of what nature could these additions be? Additions of material cannot surely be in question. We are told that salts of iron in the soil may turn a pink hydrangea blue. The iron cannot be passed on to the next generation. How can the iron multiply itself? The power to assimilate the iron is all that can be transmitted. A disease-producing organism like the pebrine of silkworms can in a very few cases be passed on through the germ-cells. Such an organism can multiply and can produce its characteristic effects in the next generation. But it does not become part of the invaded host, and we cannot conceive it taking part in the geometrically ordered processes of segregation. These illustrations may seem too gross; but what refinement will meet the requirements of the problem, that the thing introduced must be, as the living organism itself is, capable of multiplication and of subordinating itself in a definite system of segregation? That which is conferred in variation must rather itself be a change, not of material, but of arrangement, or of motion. The invocation of additions extrinsic to the organism does not seriously help us to imagine how the power to change can be conferred, and if it proves that hope in that direction must be abandoned, I think we lose very little. By the re-arrangement of a very moderate number of things we soon reach a number of possibilities practically infinite.

That primordial life may have been of small dimensions need not

disturb us. Quantity is of no account in these considerations. Shakespeare once existed as a speck of protoplasm not so big as a small pin's head. To this nothing was added that would not equally well have served to build up a baboon or a rat. Let us consider how far we can get by the process of removal of what we call "epistatic" factors, in other words those that control, mask, or suppress underlying powers and faculties. I have spoken of the vast range of colours exhibited by modern Sweet Peas. There is no question that these have been derived from the one wild bi-colour form by a process of successive removals. When the vast range of form, size, and flavour to be found among the cultivated apples is considered it seems difficult to suppose that all this variety is hidden in the wild crab-apple. I cannot positively assert that this is so, but I think all familiar with Mendelian analysis would agree with me that it is probable, and that the wild crab contains presumably inhibiting elements which the cultivated kinds have lost. The legend that the seedlings of cultivated apples become crabs is often repeated. After many inquiries among the raisers of apple seedlings I have never found an authentic case—once only even an alleged case, and this on inquiry proved to be unfounded. I have confidence that the artistic gifts of mankind will prove to be due not to something added to the make-up of an ordinary man, but to the absence of factors which in the normal person inhibit the development of these gifts. They are almost beyond doubt to be looked upon as *releases* of powers normally suppressed. The instrument is there, but it is "stopped down." The scents of flowers or fruits, the finely repeated divisions that give its quality to the wool of the Merino, or in an analogous case the multiplicity of quills to the tail of the fantail pigeon, are in all probability other examples of such releases. You may ask what guides us in the discrimination of the positive factors and how we can satisfy ourselves that the appearance of a quality is due to loss. It must be conceded that in these determinations we have as yet recourse only to the effects of dominance. When the tall pea is crossed with the dwarf, since the offspring is tall we say that the tall parent passed a factor into the cross-bred which makes it tall. The pure tall parent had two doses of this factor; the dwarf had none; and since the cross-bred is tall we say that one dose of the dominant tallness is enough to give the full height. The reasoning seems unanswerable. But the commoner result of crossing is the production of a form intermediate between the two pure parental types. In such examples we see clearly enough that the full parental characteristics can only appear when they are homozygous—formed from similar germ-cells, and that one dose is insufficient to produce either effect fully. When this is so we can never be sure which side is positive and which negative. Since, then, when dominance is incomplete we find ourselves in this difficulty, we perceive that the amount of the effect is our only criterion in distinguishing the positive from the negative, and when we return even to the example of the tall and dwarf peas the matter is not so certain as it seemed. Professor Cockerell lately found among thousands of yellow sun-

flowers one which was partly red. By breeding he raised from this a form wholly red. Evidently the yellow and the wholly red are the pure forms, and the partially red is the heterozygote. We may then say that the yellow is *YY* with two doses of a positive factor which inhibits the development of pigment; the red is *yy*, with no dose of the inhibitor; and the partially red are *Yy*, with only one dose of it. But we might be tempted to think the red was a positive characteristic, and invert the expressions, representing the red as *RR*, the partly red as *Rr*, and the yellow as *rr*. According as we adopt the one or the other system of expression we shall interpret the evolutionary change as one of loss or as one of addition. May we not interpret the other apparent new dominants in the same way? The white dominant in the fowl or in the Chinese Primula can inhibit colour. But may it not be that the original coloured fowl or Primula had two doses of a factor which inhibited this inhibitor. The Pepper Moth, *Amphidasys betularia*, produced in England about 1840 a black variety, then a novelty, now common in certain areas, which behaves as a full dominant. The pure blacks are no blacker than the cross-bred. Though at first sight it seems that the black *must* have been something added, we can without absurdity suggest that the normal is the term in which two doses of inhibitor are present, and that in the absence of one of them the black appears.

In spite of seeming perversity, therefore, we have to admit that there is no evolutionary change which in the present state of our knowledge we can positively declare to be not due to loss. When this has been conceded it is natural to ask whether the removal of inhibiting factors may not be invoked in alleviation of the necessity which has driven students of the domestic breeds to refer their diversities to multiple origins. Something, no doubt, is to be hoped for in that direction, but not until much better and more extensive knowledge of what variation by loss may effect in the living body can we have any real assurance that this difficulty has been obviated. We should be greatly helped by some indication as to whether the origin of life has been single or multiple. Modern opinion is, perhaps, inclining to the multiple theory, but we have no real evidence. Indeed, the problem still stands outside the range of scientific investigation, and when we hear the spontaneous formation of formaldehyde mentioned as a possible first step in the origin of life, we think of Harry Lauder in the character of a Glasgow schoolboy pulling out his treasures from his pocket—"That's a wassher—for makkin' motor cars"!

As the evidence stands at present all that can be safely added in amplification of the evolutionary creed may be summed up in the statement that variation occurs as a definite event often producing a sensibly discontinuous result; that the succession of varieties comes to pass by the elevation and establishment of sporadic groups of individuals owing their origin to such isolated events; and that the change which we see as a nascent variation is often, perhaps always, one of loss. Modern research lends not the smallest encouragement or sanction to the view that gradual evolution occurs by the transformation of masses of individuals, though that fancy has fixed itself

on popular imagination. The isolated events to which variation is due are evidently changes in the germinal tissues, probably in the manner in which they divide. It is likely that the occurrence of these variations is wholly irregular, and as to their causation we are absolutely without surmise or even plausible speculation. Distinct types once arisen, no doubt a profusion of the forms called species have been derived from them by simple crossing and subsequent recombination. New species may be now in course of creation by this means, but the limits of the process are obviously narrow. On the other hand, we see no changes in progress around us in the contemporary world which we can imagine likely to culminate in the evolution of forms distinct in the larger sense. By intercrossing Dogs, Jackals, and Wolves, new forms of these types can be made, some of which may be species, but I see no reason to think that from such material a Fox could be bred in indefinite time, or that Dogs could be bred from Foxes.

Whether Science will hereafter discover that certain groups can by peculiarities in their genetic physiology be declared to have a prerogative quality justifying their recognition as species in the old sense, and that the differences of others are of such a subordinate degree that they may in contrast be termed varieties, further genetic research alone can show. I myself anticipate that such a discovery will be made, but I cannot defend the opinion with positive conviction.

Somewhat reluctantly, and rather from a sense of duty, I have devoted most of this Address to the evolutionary aspects of genetic research. We cannot keep these things out of our heads, though sometimes we wish we could. The outcome, as you will have seen, is negative, destroying much that till lately passed for gospel. Destruction may be useful, but it is a low kind of work. We are just about where Boyle was in the seventeenth century. We can dispose of Alchemy, but we cannot make more than a quasi-chemistry. We are awaiting our Priestley and our Mendeléeff. In truth it is not these wider aspects of genetics that are at present our chief concern. They will come in their time. The great advances of science are made like those of evolution, not by imperceptible mass-improvement, but by the sporadic birth of penetrative genius. The journeymen follow after him, widening and clearing up, as we are doing along the track that Mendel found.

NOTES AND QUERIES.

AVES.

Norfolk Redshanks.—Reference was made in the July number of the 'Zoologist' (*ante*, p. 275) to the early appearance of some young Redshanks (*Totanus calidris*) in the east of Norfolk. As I was the actual observer, some further facts concerning this record may be appreciated by ornithologists. I found the birds under question frequenting the shore of a small, still, piece of water close to Breydon. They were foolishly tame, and on the afternoon of April 25th (1913) gave me ample opportunity for close observation. With other signs of immaturity, I then particularly noticed the *yellowish legs*. These Redshanks remained in the same locality for some few days after the 25th. Curiously enough, it was not until Mr. Gurney had noticed the entry concerning them in my diary that I realized how premature the date was for the occurrence, and now I really cannot remember whether there were three or four of them.—F. N. CHASEN (North Denes Road, Great Yarmouth).

Thrush Swimming.—As is well known, most birds can swim, at least when in peril. At Dorking one September day I saw a Thrush fall into the water about forty yards from the opposite bank, and flapping its wings on the surface and *apparently* using its legs as propellers, safely reached the bushes on the other side of the river.—W. L. DISTANT.

PISCES.

Notes by an Angler.—The following notes refer to fishing days on the River Mole, on a stretch from Gatwick to Dorking. Pliny the younger in one of his letters confesses to have turned sportsman, and writes, "I advise you whenever you hunt in future to take your tablets with you as well as your casket and flask." Substitute the words "angling" and "note-book," and this is a good angler's exhortation. The following are some of my jottings on happy days with the rod.

GUDGEON (*Gobio fluviatilis*).—This small fish is generally described as found on the bottom where the current is not too strong

and the water moderately shallow, which in a general way is true for the Mole. But there is a great exception in the broader and deeper parts of the river. For about an hour in the afternoon an angler may derive some surprise if he fishes with a line near the surface of some deep hole, say twelve to fourteen feet in depth, such a one as is in my mind at this moment. A number of small fish, Roach, Chubb, Rudd, and also Gudgeon, may then be caught, and with ease and rapidity, about two feet or less below the surface. The first Gudgeon that I took from this deep hole I thought, to my surprise, must have come from the bottom, but subsequent experience showed me that it must have followed the bait from the surface, and I have tried the experiment of shallow fishing (in the afternoon) many times since, and took Gudgeon among the other fishes. Where the stream is shallow the Gudgeon frequents the bottom in the Mole as elsewhere, but in the deeper parts it becomes a surface fish towards the afternoon.

Butterflies eaten by Bream.—I had long wondered whether lepidopterous insects could be added to the prey of our freshwater fishes, but during a long angling experience had never been able to make such an observation. On one fine morning at Dorking, and within half a hour of each other, I saw two common white butterflies fall in the river, and at once seized and swallowed by patrolling Bream.—W. L. Distant.